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THE ROLE OF ETHYLENE
IN PLANT GROWTH AND DEVELOPMENT

Frederick B. Abeles

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2

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processes, and air pollution.

CONTENTS

I. ETHYLENE AS HORMONE

Hormone physiology is concerned with the biogenesis of the hormone, what it does, how it does it, how it moves within the organism, and the nature of the processes leading to its removal as a functioning molecule. This review is concerned with the second question, that is, what is the normal role of ethylene in plant growth and development. Ethylene is different from other hormones because it is a gas. Because of this it is one of the easiest to study, since by incorporating it in the gas phase it is applied with the minimum perturbation of the plant's normal physiology. It is also easy to obtain and monitor, assuming a gas chromatograph is available, and there are none of the problems of degradation and conjugation associated with other plant hormones. Although rates of production vary from one part to another, it is produced throughout the plant and diffuses readily from the site of production to the external atmosphere. The old concept of a hormone as a substance produced in one organ and transported to another does not apply to ethylene; it may be more reasonable and simpler to define a hormone as any regulatory substance whose mode of action is unclear. Just as soon as the role of a molecule in physiology is defined it moves out of the mysterious hormone classification and is characterized as a cofactor, coenzyme, vitamin, allosteric effector, or is given some other role.

II. ROLE IN GERMINATION

Ethylene has been shown to promote the germination of wheat,[1] oat,[2] peanuts,[3-5] clover,[6] and lettuce.[7] Ethylene levels in unpolluted air are low, usually in the order of 5 ppb or less, but the levels in soil are significantly higher. Smith and Russell[8] reported that the ethylene content of aerobic soil was 0.07 ppm in the upper 15 cm but could increase to 10 ppm when the soil was soaked with water. These values are within the range for a positive effect on germination. Typical for other ethylene effects, 1 to 10 ppm saturates the requirement for ethylene in germination and 0.1 ppm is a half-maximal dose.[6,7]

The question of whether endogenous levels of ethylene are capable of promoting germination is difficult to answer because it is hard to distinguish between the ethylene synthesized prior to germination and that associated with actively growing tissue. In other words, it is hard to separate a trigger action from a by-product of the processes.

However, Esashi and Leopold[8] found that non-dormant varieties of clover produced greater quantities of ethylene than dormant ones, and similar data were obtained by Ketring and Morgan[3] for non-dormant versus dormant peanuts. An experiment by Esashi and Leopold[8] suggests that endogenously produced ethylene does have an influence on seed germination. They found that seeds placed in small containers germinated at a greater rate than those in larger containers. A similar effect was observed earlier by Toole, Bailey, and Toole.[5]

A self-regulating effect of ethylene may have an ecological effect or benefit on germination. Seeds surrounded by soil would be exposed to higher levels of ethylene than those on the surface, even though a good supply of water might be temporarily available. The observation that CO_2 also increases seed germination[5-7] suggests that plants have also adapted to high CO_2 levels in soils. Depending on the depth, moisture, and soil structure, CO_2 levels in soils vary from 0.2 to 17%.[9]

The effect of CO_2 on germination is strange in that CO_2 mimics rather than blocks ethylene action. Germination is the only process in which CO_2 fails to act as a competitive inhibitor of ethylene.

However, the action of CO_2 appears to be physiologically different from that of ethylene for two reasons. First, Toole et al.[6] reported that peanut cotyledons were etiolated in the absence of CO_2 but developed normally when it was present. Secondly, Esashi and Leopold[8] found that the CO_2 effect was additive to the ethylene effect.

The mode of action of ethylene on germination isn't clear but some observations of Ku et al.[10] and Jones[11] bear on the problem. Ku et al.[10] reported that ethylene (and CO_2) promoted the growth of rice seedlings. We have found* that ethylene had no effect, promotive or otherwise, on rice coleoptile sections; this suggests that the action of the gas is not directly on the embryo. A possible explanation suggests itself from some experiments of the effect of ethylene on α-amylase formation in another cereal, barley. Jones[11] reported that ethylene increased the rate of α-amylase secretion (not synthesis) from barley half-seeds. Using techniques essentially similar to his, we found that, although ethylene itself has no effect on α-amylase formation from rice half-seeds, it does increase the total levels of the enzyme in seeds treated simultaneously with gibberellin.* It is conceivable, then, that one explanation for ethylene

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* Unpublished results.

action during germination is to enhance the mobilization of food reserves, as opposed to any direct effect on dormancy itself. In fact, experiments with lettuce seeds demonstrated that the action of ethylene was not directed toward a release of dormancy itself, but rather toward some other processes associated with germination.[7]

III. BUD DORMANCY

Ethylene is known to have either a promotive or inhibitive effect on bud development. Generally speaking, ethylene promotes the growth of dormant buds when the gas is given to tissue for a few days and then removed.[12,13] However, an increase in ethylene production prior to bud break in these or other species remains to be demonstrated. On the other hand, the presence of high levels of ethylene prevents bud growth; the inhibition of internode elongation and leaf expansion play a primary role. Burg and Burg[14] have shown that nodal regions of pea plants produced more ethylene than internodal ones, and that the inhibition of lateral bud break by apical application of auxin was due to the increased ethylene production associated with the application of high levels of auxin. The extent to which endogenous ethylene production controls bud dormancy remains to be shown. However, the observation that removal of apical tissue causes the release of lateral buds is well known, and Abeles and Rubinstein[15] and Burg and Burg[14] have shown that decapitation also causes a decrease in the ethylene evolved from subtending tissues.

IV. ROOT GEOTROPISM

The idea that ethylene plays a role in root geotropism was advanced by Chadwick and Burg.[16,17] They envisioned that the following processes occur between placing a seedling on its side and the induction of root curvature. The gravitational stimulus causes an asymmetric distribution of auxin, followed by a rapid rise in ethylene production and subsequent inhibition of cell elongation on the lower side of the root. As soon as the root resumes its normal orientation, the auxin gradient becomes symmetrical, ethylene production slows, and the root cells resume their normal rate of elongation.

The following evidence supports the idea that ethylene does mediate root geotropism. An asymmetrical (70:30) distribution of auxin in horizontal plants has been observed by Boysen-Jensen[18] and Hawker.[19] As Chadwick and Burg[17] point out, a 90:10 ratio may be a better estimate of asymmetry if

8

only the upper and lower surfaces of the root are considered. Chadwick and Burg[16,17] have shown that low, 10^{-6} M, physiological levels of auxin are capable of promoting ethylene production in roots. Although the work was done with stem instead of root tissue, Abeles and Rubinstein[5] found a higher rate of ethylene production from the underside of horizontal bean hypocotyls. Chadwick and Burg[17] reported that ethylene control of root elongation during the first 8 hours was rapid and reversible. Both inhibition and resumption of normal growth extrapolated back to zero time after the addition or removal of ethylene. Studies with intact roots also confirmed the role of ethylene in root growth. Both CO_2 and ethylene retarded or blocked the curvature of pea roots placed horizontally. In the case of CO_2, the inhibition was due to blocking the action of ethylene produced in the lower side of the root. CO_2 itself has been shown to either promote or have no effect on root growth.[17-20] Ethylene, on the other hand, blocked geotropism because a high level or the gas would tend to mask any asymmetry of ethylene evolution.

Others, however, question the role of ethylene in root geotropism. Andreae et al.[21] reported that they were unable to observe a rapid inhibition of growth by ethylene. However, the data they presented were inconsistent. In their figure 2 the effect of ethylene extrapolates to zero time, and in the remaining figures, the control curves show a slight but distinct inhibition of growth for the first 3 hours, suggesting a possible interference of "wound" ethylene.

A more valid criticism stems from the kinetics of auxin inhibition. If ethylene did mediate the auxin effect, there should be a lag in auxin inhibition of root growth corresponding with the 30-minute lag in ethylene production observed by Chadwick and Burg.[16]

This lag is due primarily to the fact that the auxin stimulation of ethylene biogenesis is caused by the de novo synthesis of ethylene-generating enzymes.[22] Unpublished work from our laboratory* has shown that the ability of auxin to promote ethylene production from pea roots occurs only after a 60-minute lag and that actinomycin D and cycloheximide prevent the rise in ethylene evolution. However, both Andreae et al.[21] and Chadwick and Burg[17] report that the auxin inhibition of root growth extrapolates to zero time, even though the first measurements were made 2 to 3 hours after the addition of auxin. As Barkley and Evans[23] point out, even though elongation rates extrapolate to zero, short-time responses can involve a number of distinct growth rates, including inhibitions and stimulations.

In the final analysis, as Andreae et al.[21] suggested, it appears that the kinetics of curvature will determine whether ethylene does play a role in root geotropism. Chadwick and Burg[16,17] point out that the first observable curvature occurs 15 minutes after the seedling is placed on its side. This means that asymmetrical auxin distribution, increased ethylene production, and the effect of ethylene on growth must take place in this time frame.

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* Peterson, D.M.; Leather, G.R.

V. SEEDLING GROWTH

When etiolated seedlings are treated with ethylene, the new growth is reduced in length and increased in diameter. This kind of growth can be characterized as a swelling. Two examples in which swellings appear to play a role are in the growth of seedlings through the soil and in the formation of bulbs in onions and related plants. Goeschl, Rappaport, and Pratt[34] reported that a mechanical obstruction of pea seedling growth caused an increase in ethylene production. A comparison between elongation and ethylene production revealed that a decrease in elongation occurred about 20 hours after the increase in ethylene production and normal growth resumed 10 hours after the maximum of ethylene production.

Further proof for the role of ethylene in epicotyl elongation came from a comparison between seedlings growing through glass beads and those grown in the presence of 0.2 ppm ethylene. The above-mentioned authors[24] found that seedlings growing under glass beads produced ethylene at the rate of 2.1 nl/g per hour. Using the conversion figure of Chadwick and Burg[17] (1 ppm internal ethylene concentration = 6 nl/g per hour ethylene evolved), the internal levels of ethylene in the pea seedlings should have been approximately 0.29 ppm. The fact that seedlings treated with 0.2 ppm ethylene and those grown under a load of glass beads were similar in length, diameter, and volume substantiates the role of ethylene in the inhibition of growth. The practical advantages of this mode of growth to the seedling can be seen from the fact that the total force a seedling can exert is proportional to the square of the radius, and the ability to support the resulting load is proportional to the fourth power of the radius.

VI. BULB FORMATION

Recent experiments by Levy and Kedar[25] indicate that ethylene may play a role in bulb initiation of onions. They found that onions grown under short days failed to form bulbs, but when the plants were treated with Ethrel (2-chloroethylphosphonic acid), swellings at the base of the leaves, similar in appearance to normal bulbs, appeared.

VII. EPINASTY

Isodiametric enlargement of basal cells on the upper side of petioles gives rise to a characteristic curvature called epinasty. Ethylene can cause epinasty and has been implicated as a mediating factor in epinasty

induced by auxin,[26] gravity,[27] and disease.[28] However, epinasty is a complicated phenomenon not subject to simple analysis. For example, ethylene can cause leaf epinasty in an intact leaf but not when the blade portion is removed. Substitution of the blade with auxin results in epinasty once again and suggests that ethylene alone does not cause epinasty.

Lyon[29] demonstrated lateral dissymmetry of auxin in gravitationally induced epinasty with greater amounts of the hormone on the adaxial or upper surface (64:36 ratio). This cannot mean that greater amounts of ethylene are produced in the upper surface and that this is what causes the epinasty, because placing a plant in ethylene would mask any dissymmetry and would inhibit instead of promote epinasty.

Since Burg and Burg[30] found that ethylene blocks gravitationally induced auxin transport in pea stems, it might be possible to explain ethylene action in epinasty as the blocking of gravitationally induced abaxial transport but leaving the endogenous adaxial transport undisturbed. However, close analysis shows that this doesn't make sense either. Crocker, Zimmerman, and Hitchcock[31] reported that ethylene would not cause epinasty in tomato plants when they were turned upside down. If ethylene interferes with gravitational transport, then inverted tomato plants should have epinastic leaves for two reasons: first, ethylene should have inhibited abaxial transport, and secondly, the normal gravitational pull on auxin, if it can be thought of that way, was blocked anyway.

VIII. MOTOR TISSUE MOVEMENT

Jaffe[32] has presented evidence that ethylene may participate in rapid movements of motor tissue from a variety of plants. He found that leaves of *Mimosa* *pudica* fell more rapidly when the pulvinus was treated with Ethrel. When pinnules of *Albizzia* *julibrissin* were exposed to red light, which promoted closure, ethylene production was promoted. Far-red light, which prevents closure, retarded ethylene evolution. Application of Ethrel to the upper surface of the tertiary pulvini induced closure. Jaffe[32] also observed that ethylene production from pea tendrils was greater from coiling tendrils than from those at rest, and that topical application of Ethrel to the inside or ventral surface induced coiling.

IX. HOOK OPENING

The germination of many seeds involves the penetration of the soil with
a hook-shaped organ. Once the seedling breaks the surface, the hook opens,
the hypocotyl ceases to elongate, and the primary leaf starts to expand.
Straightening of the hook is due to the rapid elongation of the cells on
the inner side of the hook and is under the control of at least three
factors: light, auxin, and ethylene.[33] Regulation of hook opening by
ethylene depends on a number of factors, including sensitivity of the
tissue to the gas as well as regulation of ethylene production. Burg and
Burg[34] have demonstrated that dark-grown seedlings are more sensitive to
ethylene than those exposed to light. The production of ethylene by seed-
lings falls off as they penetrate the soil because of a decrease in
mechanical resistance[24] and exposure to light.[35,36] The light effect appears
to be mediated via phytochrome, since red light decreases ethylene production
and far-red light causes a return to the normal rate of synthesis.[37]
Ethylene causes hooks to close, and penetration of the seedlings through
the soil causes a reduction of ethylene evolution, so the simple explanation
for hook opening is a reduction of ethylene in the hook region. However,
although hook opening appears to be a simple process, a number of factors
are involved and no one regulator has complete or primary control.

For example, the effect of red light is more than ~ reduction of
ethylene evolution. When hooks are irradiated with red light they normally
open and when treated with ethylene they close. However, contrary to
expectation, ethylene has a greater effect on hooks exposed to red light
than on those left in the dark.[37] This is opposite to the anticipated
result, which would have been a greater effect of ethylene on dark controls.

Another unresolved problem is based on the question of kinetics.
Reduction of ethylene production following red light treatment occurs
after a 6-hour lag period.[37] Changes in hook opening, however, take place
after 4 hours.[38] Kang and Ray[38] believe that part of the discrepancy is
due to light-induced CO_2 production that occurs after a 2-hour lag.
Finally, even though there is a 2-hour lag between ethylene treatment and
growth inhibition, there was no lag between auxin application and inhibition
of hook opening.[37]

X. ETHYLENE IN SOIL

Unlike aboveground portions of plants, where free gas exchange tends to
keep ethylene levels at a minimum, the soil acts as a barrier to diffusion
and ethylene levels can rise to physiologically significant levels. The
observation of Smith and Russell[8] that ethylene levels rise rapidly in wet
soils suggests that the gas may play a role in the water relationships of

plants. We know from the work of the Boyce Thompson group[39] that ethylene has a number of striking effects on root physiology. They reported that ethylene induced root formation from preexisting roots, stems, and occasionally leaves from a wide variety of plants. Similar to its effects on bud break, ethylene had to be present for 1 or 2 days and then removed to permit elongation of the newly initiated root. They observed that ethylene increased the potential water-absorbing capacity of roots by inducing root-hair formation. They also observed that ethylene altered the normal geotropic response of the root, with the result that plants growing in ethylene had their roots growing up out of the soil.

It is conceivable that these responses would have some ecological benefit to roots growing under wet and consequently high ethylene conditions. As the ethylene levels rose the roots would automatically increase the number of absorbing structures (branch roots and root hairs), slow their rate of elongation, and change their normal geotropic response. Under drier conditions, the ethylene concentration would be less, and roots would tend to elongate downward with a minimum of branching.

XI. ROLE IN FLOWERING

We know little about the role of ethylene in flowering other than some observations that the gas has some interesting effects on the processes. Ethylene can promote flowering, notably in bromeliads,[40,41] inhibit flowering,[42] or change the sex expression of monoecious plants such as cucurbits.[43]

XII. PHYTOGERONTOLOGY

Phytogerontology is a term that describes, in its broadest sense, maturation, ripening, aging, and senescence. Maturation involves those processes associated with fulfillment of predetermine form or function; ripening, a special case involving the development of optimal qualities for consumption as seen from an anthropomorphic point of view; aging, those processes that start, stop, or change direction in time without reference to any particular event; and senescence, the physiology of death, or those processes associated with the termination of the biochemical life of cells. Ethylene plays a role in some of these processes, notably floral senescence, fruit ripening, and abscission.

Blossoms of a variety of plants produce ethylene and senesce or fade when exposed to ethylene. In addition, CO_2, a competitive inhibitor of

ethylene, tends to delay the deterioration of blossoms.[44-46] The participation of ethylene in the fading of orchids was demonstrated by Burg and Dijkman.[44] They found that pollination, auxin treatment, and removal of the pollinia, all of which hasten fading, increased ethylene production. They were able to correlate the fading with the peak of ethylene production. In untreated flowers, a rise in ethylene production also coincided with fading. As in the case of fruits, Burg and Dijkman[44] found that flowers given a prior treatment of ethylene produce additional quantities of the gas in an autocatalytic fashion. They believe that these results suggest that the fading response spreads outward from the orchid column because each cell triggers its neighbor to produce ethylene by gassing it with the hormone. They concluded that the normal senescence of orchids involves transfer of pollen to the stigma, which then produces large quantities of ethylene in response to the auxin in the pollen, diffusion of the ethylene from the site of production to neighboring cells where the gas induced additional ethylene production, and concomitant fading.

The part that ethylene plays in ripening and abscission has been reviewed recently by others.[47-49] Basic observations lead to the idea that ethylene is a ripening and abscission hormone.

First of all, addition of the gas sets the process into motion or accelerates it. At this point it is important to note that the levels of ethylene used to promote ripening and abscission are similar to those used to induce other processes, i.e., half-maximal dose ≈ 0.1 ppm and a saturating dose ≈ 10 ppm. The concentrations of ethylene analogues such as carbon monoxide, propylene, and acetylene used to induce ethylene responses are higher and serve as a guide in identifying a typical ethylene-mediated process. There are examples of ethylene action that do not conform with the dose and analogue rule;[50] these suggest that dose response and analogue data should be essential parts of experiments purporting to show plant growth and development regulation by ethylene.

Secondly, removal of ethylene or blockage of its action by CO_2 slows ripening or abscission. The degree of success from removing ethylene or adding CO_2 varies from partial retardation to the extreme case where it was possible to store bananas for many months under a partial vacuum.[51]

There are two distinct ways by which ethylene can regulate ripening and abscission or, for that matter, any process, under natural conditions. The first is an increase in ethylene concentration in the tissue and the second is an increase in sensitivity to the gas that may already be present. It seems reasonable that some combination of either case would also be important. Examples of data showing a rise in ethylene production prior to ripening[52,53] and abscission[54] have been presented. Examples of increasing sensitivity to ethylene with time have also been shown.[55,56]

It should be stressed that ethylene is not alone in its control of abscission and ripening, and that other hormones, notably aging retardants such as auxin and cytokinins, are involved. To complicate matters further, it is apparent that ethylene can also act as an aging hormone and actually increase the sensitivity of plant tissue to ethylene.[57]

XIII. ETHYLENE AS AIR POLLUTANT

The role of ethylene as an air pollutant has received little attention compared with other pollutants such as carbon monoxide, nitrogen dioxide, sulfur dioxide, ozone, and peroxyacetyl nitrate. What makes ethylene such an unusual and dangerous pollutant is the fact that it is a plant hormone and many of its detrimental effects are associated with the disruption of the normal hormonal regulation of the plant. Some of the important effects of ethylene on plants and the amounts required to cause a response are well known. However, little is known concerning levels of ethylene in the air, the major sources of ethylene, and the mechanisms by which ethylene is removed or destroyed.

Reports of damaging effects of ethylene on plants have increased since the early observations of detrimental effects of illuminating gas on plants.

Some recent examples of plant damage attributed to ethylene include losses of $70,000[58] to $150,000[59] by flower growers in San Francisco and Chicago. In 1970, growers in Pennsylvania reported that ethylene damages to flowers totaled $9,200 of a total loss of $3.5 million.[60] Only recently have workers concerned with air pollution begun to study ethylene levels in the atmosphere, and preliminary reports show damaging levels of ethylene, 0.07 to 0.20 ppm, within urban centers.[58] A major contributor of ethylene to the air is the automobile. Along with other plant-damaging gases, we have found that automobile exhaust contains 500 ppm ethylene. This is far higher than other plant-damaging constituents of exhaust such as CO (100 ppm), NO_2 (0.1 ppm), and, after irradiation, O_3 (0.2 ppm). Assuming the exhaust could be contained, we estimate that an idling car produces enough ethylene in 1 minute to defoliate a full-grown tree. The influence of automobiles can be seen in the following figures. We have found that air in a local shopping center parking lot contained 0.05 ppm ethylene, along a local highway 0.010 ppm, and in an intersection 0.10 ppm ethylene. These figures are in contrast to 0.001 to 0.005 ppm in rural areas.

Another source of ethylene is industry. Ethylene concentrations downwind of industrial polyethylene plants ranged from 0.04 to 3.0 ppm and effects on plants were noticeable as far as 2 miles from the plant.[61]

Burning plant material produces large amounts of ethylene. We have found that cigarette smoke contains between 500 and 1,000 ppm ethylene. Interestingly enough, filters, charcoal or otherwise, have little effect on the amount of ethylene produced by a smoker.

To summarize, we know that low levels of ethylene (0.1 ppm) cause plant damage by defoliation, abnormal growth, and loss of blossoms. An exhaustive study of detrimental effects of ethylene to 114 agronomic

plants was published by Heck and Pires.[62] On the other hand, we know little about the ethylene part of the carbon cycle in nature. Little information is available on the relative contribution of ethylene to the air by man as opposed to that by plants. Similarly, we have scant knowledge on the removal of ethylene by destruction via ozone, UV light, and other mechanisms. We have no idea how much ethylene we can add to the air and still expect natural removal mechanisms to keep ethylene at safe or at least tolerable levels.

Apparently it has become so difficult to raise natural plants in urban areas that the plastic variety has taken over in some form of unnatural ecological succession. On the assumption that the average citizen spends a dime a year on plastic plant replacements, the American public is paying $20 million to overcome the loss of plants to air pollutants. It is ironic that the plastic most widely used is polyethylene.

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